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General discussion:

Patterning in mussel beds explained by the interplay of multilevel selection and spatial self-organization

Monique de Jager

General Discussion

Nature often is amazingly complex. A wide variety of complex spatial patterns can be found throughout nature, ranging from the organization of molecules (Hogeweg & Takeuchi, 2002) to the formation of regular, self-organized patterns at the scale of entire ecosystems (i.e. Klausmeier, 1999; Rietkerk *et al.*, 2004a&b; Van de Koppel *et al.*, 2005 & 2008; Eppinga *et al.*, 2009). Self-organized patterns in ecosystems develop from the actions of and interactions between organisms. The behaviour of these individuals is an important driving force behind spatial self-organization. Yet, this behaviour has evolved to its present form partly as a consequence of this self-made environment. Hence, feedback between self-organization of ecosystems and the evolution of individual behaviour is quite apparent. Nevertheless, scientists generally research self-organization and evolution separately and thereby disregard this feedback (but see Kéfi et al., 2008; Xavier et al., 2009). Neglecting eco-evolutionary feedbacks in self-organized ecosystems might have considerable consequences, especially when incorrect conclusions are drawn from ecological models.

Throughout the chapters of this thesis, I have demonstrated that close feedback between the evolution of individual behaviour and the spatial complexity of their community is essential to explain the cooperative behaviour and movement strategies of organisms. To examine eco-evolutionary feedbacks in self-organized systems, I used intertidal mussels as my main experimental system and model template. By moving into clumps and attaching to close neighbours, mussels build extensive spatial networks that minimize losses due to predation and wave dislodgment (Hunt & Scheibling, 2001, 2002; Van de Koppel *et al.*, 2005, 2008). Mussels were found to apply a specific movement strategy – a Lévy walk – that maximizes the speed of pattern formation (**Chapter 2**). The active aggregation of mussels into labyrinth-like patterns promotes the evolution of between-mussel cooperation, where mussels affix themselves with byssus threads to neighbouring conspecifics to decrease dislodgment risk by wave stress and predation (**Chapter 5**). In turn, the labyrinth-like pattern is the consequence of multilevel selection processes acting on the joint evolution of aggregative movement and between-mussel cooperation (**Chapter 6**). The results shown in this thesis leave me to conclude that feedback between ecological and evolutionary processes are fundamental to self-organization of mussel beds and, most likely, to many other complex ecosystems.

In this chapter, I discuss the most important results presented in my dissertation. A detailed account of the work described here can be found in the previous chapters. In my thesis, I have focused mainly on the effect of eco-evolutionary feedback on two behaviours: movement and cooperation. In the following sections, I first discuss how mussel movement strategies are affected by self-made environmental complexity. Second, I deliberate on the effect of the self-generated spatial population structure on the evolution of cooperation and, in turn, on the influence of evolution on spatial self-organization. In the final section, I review the main conclusions that can be drawn from my findings. In general, my results suggest that eco-evolutionary feedbacks have important consequences for both the behaviour of individuals and the complexity of ecosystems.

Ecological interactions drive animal movement patterns

How feedback leads to Lévy walks

Over the past years, ecologists have found a growing body of empirical evidence on Lévy walks in animal movement patterns. A Lévy walk is a random search strategy which alternates many small steps with occasional long moves and is therefore superdiffusive by nature (Viswanathan *et al.*, 2000; Codling *et al.*, 2008). With modern technology advancing GPS tracking systems and high-resolution imaging, superdiffusive Lévy-like movements have been observed in a wide variety of species, such as soil amoebas, bees, seabirds, seals, spider monkeys, predatory fish, and even humans (Heinrich, 1979; Viswanathan *et al.*, 1996; Sims *et al.*, 2000; Austin *et al.*, 2004; Ramos-Fernandez *et al.*, 2004; Bertrand *et al.*, 2007; Reynolds *et al.*, 2007). One of the main concerns about these empirical findings is that the notion of Lévy movement being a widespread phenomenon clashes with classical optimal foraging theory. In theory, an organism adopts a certain movement strategy if it optimizes the individual's search efficiency. Computer simulations have shown that Lévy walks are only optimal under highly specific conditions, which are quite rare in nature (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005; Sims *et al.*, 2008; Bartumeus, 2009; Reynolds & Bartumeus, 2009). Therefore, Lévy-like movement should not be as omnipresent as is suggested by the broad range of empirical studies. How and why Lévy walks have evolved in these systems is an important question that, until now, has remained unanswered (Reynold & Rhodes, 2009).

The theoretical models predicting the rare occurrence of Lévy walks in nature generally disregard some key aspects of standard animal life. For one, most animals are not alone; they often share their habitat and resources with other individuals. Studies on the search efficiency of different movement strategies all base their conclusions on models of single individuals, without any interference of other organisms. Another essential aspect that is frequently overlooked concerns movement of the resource. By taking these ecological interactions in account, other conclusions might be drawn than those found in previous papers (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005; Sims *et al.*, 2008; Bartumeus, 2009; Reynolds & Bartumeus, 2009). Furthermore, an examination of eco-evolutionary dynamics might aid in understanding why many animal species are moving in a Lévy-like fashion. In contrast to earlier models of search efficiency, I incorporate natural encounters with other moving individuals in my individual-based model and thereby examine search efficiency within a more realistic setting.

In **Chapter 2** of this thesis, I demonstrate how Lévy walks in mussel movements may have evolved through feedback between mussel movement and spatial patterning. Using mesocosm experiments, I observed mussels moving in a Lévy-like fashion when solitarily searching for conspecifics. Whereas previous studies on seach efficiency have disregarded most ecological encounters (Viswanathan et al., 1999; Bartumeus et al., 2005; Sims et al., 2008; Bartumeus, 2009; Reynolds & Bartumeus, 2009), I show that interactions with the biotic environment are of key importance to explain the occurrence of Lévy walks in mussel beds. Lévy movement can result from feedback between mussel movement behaviour and self-organized environmental complexity. Mussels that efficiently move into an aggregation save valuable time and energy: speeding up pattern formation decreases the time spend being vulnerable to predation and wave disturbance, and limited displacement reduces the energy spend on movement. In self-organized mussel beds, a Lévy walk is a very efficient random search strategy (see Fig. 2.2). Individuals that use an efficient search strategy, such as a Lévy walk, are likely to gain higher fitness over less efficient conspecifics, thereby increasing the frequency of efficiently moving individuals in the next generation. Simultaneously, pattern formation is accelerated with each increase in Lévy walkers within the population, which again enhances fitness advantages of efficient individuals. Overall, an eco-evolutionary feedback can explain how individual search strategy and large-scale, self-organized pattern formation leads to the evolution of Lévy-like movement in intertidal mussel beds.

Although I address a specific study system, the assumption that movement strategies can evolve through eco-evolutionary feedback may be broadly applicable. By replacing the externally determined environment – which has been the default template in studies on search efficiency – with an environment that is to a large extent shaped by the organisms themselves, Lévy walks may be found within a much broader range of conditions than was previously believed. This feedback between animal movement and environmental heterogeneity provides a potential explanation for the numerous empirical observations of Lévy walks throughout nature (Ramos-Fernandez *et al.*, 2004; Reynolds *et al.*, 2007; Sims *et al.*, 2008; Humphries *et al.*, 2010). Because animal movement patterns are for a substantial part reflected in the spatial distributions of their resources (Adler *et al.*, 2001; Boyer & Lopez-Corona, 2009), eco-evolutionary interactions between animal movement and environmental complexity are not limited to aggregation with conspecifics, but also occur in the search for resources shared with conspecifics. My study reveals that eco-evolutionary feedback between animal movement and habitat complexity is of key importance in understanding both the evolution and the ecology of animal movement strategies.

A close encounter with Brownian motion

Having a sufficiently accurate representation of animal movement in ecological models is of crucial importance for the truthfulness of model results. Although previous studies have shown the occurrence of superdiffusive movement in many animal species (Ramos-Fernandez *et al.*, 2004; Klafter & Sokolov 2005; Reynolds *et al.*, 2007; Sims *et al.*, 2008; Humphries *et al.*, 2010), normal diffusion – which is based on Brownian movement patterns – remains the default template for animal movement in most ecological models (Skellam 1951; Kareiva & Shigesada 1983; Benhamou 2007; Sims *et al.* 2008; Edwards *et al.* 2012). The most curious thing about the use of diffusion as a description of animal movement is that it (i) is based on the generality of the physical process of diffusion rather than on empirical observations of animal movement and (ii) that it is used as being density-independent, which contradicts the original mechanism as put forward by Einstein, where interactions between particles generate Brownian motion (Einstein, 1905; Langevin, 1908).

Similar to Brown's observations of pollen grains moving in a Brownian fashion (Brown, 1828), we observed mussels moving in Brownian patterns, especially when found in high density mussel clumps. Albert Einstein explained the Brownian movements of dissolved particles like pollen grains as the consequence of collisions with water molecules (Einstein, 1905; Langevin, 1908). In **Chapter 3** of this thesis, I demonstrate that animal movements are similarly affected by their environment, as intended steps are prematurely ended whenever an obstacle, such as a resource or predator, is encountered.

Our findings have some major implications for current ecological modelling. First, Brownian motion should no longer be used as the default animal movement pattern, because it is not necessarily the intrinsic movement strategy for many animals (Klafter & Sokolov 2005). Second, animal movement should be described as a density-dependent process. Using a simple model, I have shown how *any* intrinsic movement pattern can become Brownian-like in resource-rich environments. My own empirical observations as well as those of others of animals displaying Lévy-like movement in areas with low resource density and Brownian movement patterns in dense environments further confirm that animal movement is a density-dependent process (Bartumeus *et al.*, 2003; De Knegt *et al.*, 2007; Humphries *et al.*, 2010; Humphries *et al.*, 2012). As Brownian motion is currently used as a default template of animal movement, ecological models of resource-poor habitats might strongly deviate from reality. A better understanding of the interaction between ecological encounters and animal movement is needed to improve theoretical models and to explain how animal movement patterns may influence natural processes.

Using ecological interactions to identify real Lévy walks

Whether the superdiffusive movement patterns observed in nature are actual Lévy walks or consist of multiple different movement modes is currently highly debated (Benhamou 2007; Petrovskii *et al.*, 2011; Jansen *et al.*, 2012; De Jager *et al.*, 2011). Researchers argue that the power law distributions that indicate a Lévy walk may actually be composed of a collection of multiple movement strategies (Benhamou 2007; Petrovskii *et al.*, 2011). For instance, the Lévy-like shape of a step length distribution could be an artefact of pooling the movement trajectories of different individuals (Petrovskii *et al.*, 2011). Analysis of single movement paths, as I did in **Chapters 3** and **4**, can prevent this confusion. Furthermore, a movement trajectory that seems Lévy-like might be generated by a composite movement strategy, where an organism shifts from one movement mode to another with changing environmental conditions, such as ecological encounters (Jansen *et al.*, 2012; De Jager *et al.*, 2012b). Using the traditional approach of fitting movement strategies to step length distributions, one cannot distinguish between true Lévy walks and composite multi-scale walks. In **Chapter 4** of this thesis, I am able to differentiate Lévy-like movement patterns from composite Brownian walks by examining the overlap between ecological encounters and clusters of small steps. A characteristic of Lévy walks is that clusters of small steps arise at random locations, irrespective of the underlying resource distribution. In contrast, a composite walk will result in small-step clusters only at resource patches. By recording the frequency of small step clusters coinciding with food patches, I demonstrated that mud snails are using a Lévy-like search strategy instead of a composite Brownian walk. We observed clear clusters of local search on bare substrate, and in bare areas in between food patches, despite the absence of food that was presumed to trigger local search. In all cases where both the movement path and resource availability can be recorded, this novel technique can help gaining insight in the composition of the used movement strategy. The additional information obtained from recording ecological encounters can be of key importance when disentangling different movement strategies. Using this novel method, I can validate that Lévy walks are intrinsic strategies rather than a mixture of reactions to a complex environment. This result changes our understanding of Lévy movement substantially, especially for those who did not believe that these scale-free strategies could exist.

Eco-evolutionary feedback drives spatial self-organization

How cooperation is affected by spatial population structure

The evolution of cooperation is one of the most frequently investigated enigmas in evolutionary ecology (Doebeli & Hauert, 2005; Lehman & Keller, 2006; West, Griffin & Gardner, 2007, 2008). It is common knowledge that spatial population structure can affect the evolution of cooperation through the clustering of cooperative relatives (Nowak & May, 1992; Vainstein & Arenzon, 2001; Ishibuch & Namikawa, 2005; Zhang *et al.*, 2005; Kun *et al.*, 2006; Ohtsuki *et al.*, 2006; Hui & McGeoch, 2007; Kéfi *et al.*, 2008; Szamado *et al.*, 2008); however, it is not straightforward how spatial structure can affect cooperation when offspring is dispersed over a wide range rather than locally. In game theory, where cooperative strategies are played out against each other, theorists generally assume local interactions and local dispersal of cooperative strategies. Yet, many species that indeed interact locally, still disperse over a wide range (Godfrey & Kerr, 2009). Hence, current models are insufficient in explaining the influence of active aggregation on the evolution of cooperation in populations with wide-ranging dispersal.

In **Chapter 5** of this thesis, I demonstrate that local dispersal is not a prerequisite to find an effect of spatial population structure on the evolution of dispersal. As mussels aggregate into patterned mussel beds, they actively promote cooperation between unrelated conspecifics. Taking cooperation in mussel beds as an example, I suggest that active movement into spatial patterns can be a fundamental solution to the question of how cooperation can evolve in species with wide ranging dispersal. Indeed, many natural populations seem to be spatially aggregated (Bel'kovich, 1991; Heppner, 1997; Camazine *et al.*, 2001; Parrish *et al.*, 2002; Bonner, 2009); finding out how spatial heterogeneity can alter an individual's cooperative investment for any of these species would be of great interest to those who seek the holy grail of the evolution of cooperation.

Spatial self-organization causes and results from the interplay of multilevel selection and joint evolution

Models explaining ecological or evolutionary processes should be sufficiently simple to deliver understandable results and limit computational time. Yet, they should not be too simple, in which case incorrect conclusions might be drawn. For instance, overly simplistic models of search efficiency could not explain the widespread prevalence of Lévy walks in nature, as I argue in **Chapter 2** (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005; Sims *et al.*, 2008; Bartumeus, 2009; Reynolds & Bartumeus, 2009). Similarly, models of the evolution of cooperation are also generally based on basic assumptions that are rarely met in real world systems, and may therefore give incorrect results. For example, the occurrence of lattice-structured populations in nature is definitely not as omnipresent as the prevalence of theoretical cooperation studies that use lattice-structured models might suggest (i.e. Nowak & May, 1992; Lindgren & Nordahl, 1994; Brauchli, Killingback, & Doebeli, 1999).

In models of cooperation, we often neglect the fact that most organisms are mobile and can decide on where and when to aggregate or cooperate. Moreover, the decision to aggregate is a behavioural strategy which can, or even has to evolve simultaneous with cooperative behaviour. In this thesis, I show that this joint evolution of movement and cooperation leads to the emergence of different large-scale patterns than when only a single trait is involved. Yet, my work revealed that multilevel selection provided a superior explanation of the patterns that we observe in real mussel beds. The spatial structure that emerges within the population can be of great importance for the survival of the organisms, and adds another – generally neglected – level of selection. To enhance our understanding of cooperation in nature, case-specific, realistic models are needed that are more specifically tailored to a particular real-world system.

In **Chapter 6** of my thesis, I demonstrate how the interplay between movement and cooperative behaviour generates an additional level of selection emerging from self-organization, which provides a superior explanation for labyrinth-like patterns observed in mussel beds. Using a novel technique, I show that joint evolution of two traits can result in different evolutionary stable strategies than when only a single trait is allowed to evolve. This feedback between the evolution of one trait and the evolution of another trait can give rise to strategies that considerably deviate from the conclusions drawn with a single-trait model. I illustrate this by comparing the resulting aggregative movement behaviour of mussels – which for a large part drives self-organized patterning of mussel beds – between a model that involves a constant level of cooperation and one that includes the evolution of both cooperation and movement. Although I use two jointly evolving traits as an example, it is highly probable that more traits evolve simultaneously; it would be a great challenge to model joint evolution of more than two traits.

The joint evolution of aggregative movement and cooperative behaviour in mussels underlies the emergence of spatially patterned mussel beds. Due to the structure of these spatial patterns, self-organization in mussels gives rise to a second level of selection: selection at the clump level. With a simple field experiment, I demonstrated that small clumps of mussels are more easily dislodged than large clusters, which indicates that clump size affects mussel survival. By including clump-level selection in my model of joint evolution, labyrinth-like patterns emerge more frequently from the joint evolution of movement and cooperation than when only considering individual-level selection. This result indicates that selection at higher levels than the individual can be of great importance for the fate of the entire population; also, it shows that overlooking mechanisms of selection can have vast consequences for the accuracy of model outcomes.

In the end…

Spatial patterning is ubiquitous in nature and is known to emerge from self-organization in many ecosystems (Klausmeier, 1999; Mistr & Bercovici, 2003; Rietkerk *et al.*, 2004a; Rietkerk *et al.*, 2004b; Van de Koppel *et al.*, 2005; Van de Koppel & Crain, 2006; Van de Koppel *et al.*, 2008; Eppinga *et al.*, 2009). Patterns as diverse as gaps, spots, labyrinths and stripes can be generated by simple interactions between organisms and may enhance the system's resilience. Ecological models have been created to increase our understanding of self-organization in patterned ecosystems and to predict how these systems will react to changes in environmental conditions (Rietkerk *et al.*, 2004). Yet, by disregarding evolution of self-organizing traits, incorrect conclusions may be drawn from these models. By taking evolutionary processes into account, I demonstrate that eco-evolutionary feedback is of key importance for spatial patterning in self-organized ecosystems and their response to environmental changes. Because evolutionary adaptation can change interactions between organisms, it may also affect the spatial complexity of ecosystems. In turn, spatial patterns are in part responsible for the fitness differences between individuals, leading to the next adaptation. Within this feedback, complex dynamics can arise, such as the joint evolution of multiple traits or the emergence of a higher-order level of selection through self-organization into large-scale patterns. Understanding eco-evolutionary dynamics is of crucial importance if we want to predict how ecosystems respond to man-made changes to the environment, such as accelerated global warming or habitat fragmentation. The research presented in this thesis will provide us more insight into eco-evolutionary feedbacks in self-organized ecosystems and will hopefully be an inspiration for future research within this exciting field of science.

R

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Summary

Spatial patterns in natural systems may appear amazingly complex. Yet, they can often be explained by a few simple rules. In self-organized ecosystems, complex spatial patterns at the ecosystem scale arise as the consequence of actions of and interactions between organisms at a local scale. Aggregation into large-scale patterns may, however, also affect the survival and fitness of individuals within the ecosystem. As a consequence, pattern-producing behaviour in turn may have evolved as an adaptation to this self-generated environment in what is called an eco-evolutionary feedback process. Strikingly, both empirical and theoretical studies on eco-evolutionary feedbacks in self-organized ecosystems are rare. In this dissertation, I investigated the interplay between the ecological process of pattern formation and the evolution of two patterning-related traits: movement and attachment.

I investigated the interplay between the evolution of self-organizing behaviour and the emergent large-scale patterns by performing both ecological experiments and eco-evolutionary computer simulations. For this purpose, I used mussel beds as my main model system. On intertidal sandbanks, young mussels move into labyrinth-like patterns after settlement. Mussels need sufficient neighbours in close proximity to decrease the risk of being dislodged by wave stress or predation. To accomplish this, mussels attach a glue-like substance called byssus threads to other individuals, and form dense clumps. However, gaps in between dense mussel clumps are needed to reduce competition for suspended algae. Because competition occurs over a larger range than attachment, self-organized patterns emerge in the mussel bed in the form of regularly spaced, labyrinth-like strings. The formation of labyrinth-shaped patterns increases the within-clump density of mussels while keeping the long-range mussel density low enough to prevent food competition. Two behavioural traits are mainly responsible for self-organization in mussel beds: movement and attachment. Without movement, mussels cannot search for conspecifics to aggregate with; without attachment (in the form of byssal threads), self-generated spatial patterns will not last very long, as unattached individuals are easily dislodged by waves. Investigating the eco-evolutionary feedback between mussel bed formation and the evolution of

movement and attachment can provide us with interesting insights into eco-evolutionary feedbacks in self-organized ecosystems in general.

Using movement trajectories recorded during mesocosm experiments, I observed that mussels use a particular movement strategy. Movement patterns of solitary mussels are similar to a Lévy walk, where many short steps are alternated with very long moves. Lévy walks are frequently observed in nature, yet theoretical models suggest that habitats in which Lévy walks are optimal are rare, as Lévy walks are only optimal when resources are scarce and heterogeneously distributed. In **Chapter 2**, I argue that the occurrence of Lévy-like movements in mussel beds is due to the eco-evolutionary feedback between self-organized pattern formation and mussel movement. To prove this hypothesis, I simulated mussel bed formation with an individual-based model, where I varied the movement strategy used by the virtual mussels between model runs. The results of these simulations show that a spatially patterned mussel bed is generated most efficiently when mussels make use of a Lévy walk. Further evolutionary analyses, where I test for the invasion success of mutant movement strategies in a mussel population in which all other individuals adopt a resident movement strategy, demonstrate that Lévy walks evolve in my simulated self-organized mussel beds. Because Lévy walks accelerate pattern formation and the spatial pattern in turn increases the survival of these Lévy walkers, my results suggest that, in mussel beds, Lévy walks evolve through an eco-evolutionary feedback between mussel movement and self-organized patterning. Although my model is specifically designed to simulate mussel movement in self-organized mussel beds, the conclusions drawn from this study may explain why Lévy walks are found under much broader conditions than is currently explained in mathematical models.

Despite the increasing prevalence of observations of Lévy walks in nature, empiricists more and more notice that organisms might do a Lévy walk in one environment, but a Brownian walk in another. Lévy walks are frequently observed in the movement patterns of organisms that are searching for resources in resource-poor habitats, whereas their movements appear more Brownian-like, with more intermediate-sized steps and fewer large moves, in resource-rich areas. This phenomenon is often explained as an active switch in movement strategy to optimize search efficiency in both environments. Opposing this view, I hypothesized in **Chapter 3** that the intrinsic movement strategy does not change but rather that the observed movement pattern is the consequence of interactions with the environment. Following Einstein's perspective on Brownian motion in atoms and molecules, I argued that collisions with other objects such as resources or conspecifics causes a move to be prematurely ended. In areas with few objects to encounter, an organism's movement pattern would not be unrecognizably altered. In dense environments, however, the frequent occurrence of encounters transforms any movement strategy into a Brownian-like pattern. By analysing mussel movement in five different density treatments, I show that observed movement patterns become more Brownian-like with increasing mussel density. In **Chapter 4**, I found similar results for the movements of mud snails. I verified that this shift to Brownian motion is caused by collisions with conspecifics by disentangling truncated steps and moves into free space, demonstrating that the movement strategy does not change when only considering non-truncated steps. With individual-based model simulations, I showed that an active shift from Lévy to Brownian motion with increasing mussel density is unnecessary, as Lévy walks are equally efficient as Brownian movement in creating spatially patterned mussel beds at high mussel densities. Furthermore, I analytically confirmed the hypothesis that any movement strategy becomes more Brownian-like with increasing encounter rates using a simple argument. My results suggest that observed Brownian patterns in the movement trajectories of animals in their natural habitat can be the consequence of superdiffusive intrinsic movement that is altered by target density.

Whether Lévy walks observed in nature are actual Lévy walks or the product of a mixture of different strategies (a 'composite Brownian walk') is currently under debate. Using traditional methods, one cannot distinguish between the two movement types. In **Chapter 4**, a novel technique is demonstrated that helps distinguishing between true Lévy walks and composite movement strategies, by examining whether clusters of small steps coincide with resource patches (which would be indicative of a composite Brownian walk). Using a mud snail experiment as an example, it was shown that local search clusters are not only produced in food patches but also on bare soil, demonstrating that true Lévy walks may indeed exist in nature. The ability to extract intrinsic movement strategies from observed movement patterns (**Chapter 3**) and to distinguish between different movement strategies (**Chapter 4**) can have great implications for the representation of animal movement in ecological modelling: the use of Brownian motion as a default template for animal movement is not always justifiable and should be replaced by a more realistic, density-dependent type of movement template.

Mussels, as well as many other organisms, actively aggregate into groups, where they cooperate with neighbouring conspecifics. Because cooperation can be exploited by individuals that do not contribute, the widespread occurrence of cooperation in nature remains puzzling. Theoretical studies have shown that the spatial structure of a population can promote the evolution of cooperation. However, these studies consider local dispersal to be the driving factor behind both the spatial patterning and the occurrence of cooperation, thereby disregarding the fact that many species disperse over a wide range and yet cooperate locally. In **Chapter 5**, I demonstrated how spatial population structure affects the evolution of investment into byssal thread attachments in spatially patterned mussel beds. Using a simple model, I showed that active aggregation into dense mussel clumps gives rise to the highest levels of cooperativeness over a wide range of environmental stress. These results suggest that active clustering can promote the evolution of cooperation even when offspring are widely dispersed.

Cooperation and aggregative movement are two fundamental behaviours that form the foundation of self-organization in mussel beds. Without movement into clusters, mussels are unable to attach their byssus threads to neighbouring conspecifics, and without cooperation, movement into clusters would be a useless endeavour. Because movement and cooperative behaviour are quite dependent on one another, evolution of one of these traits is likely to affect evolution of the other and, subsequently, the spatial pattern that will be generated in the mussel bed. In **Chapter 6** of this thesis, I showed that the joint evolution of cooperation and aggregative movement can result in differently patterned mussel beds than when only one of the two behaviours is allowed to evolve in isolation. In most evolutionary models, evolution of other than the one focal trait is habitually disregarded; my results demonstrate that this may lead to drawing the wrong conclusions.

The self-organized pattern that emerges from the individuals' movement and cooperation in turn also affects the persistence of mussel clumps. With a simple field experiment, I showed that not only inadequately attached mussels can become dislodged by wave stress or predation, but that similarly, small mussel clumps are also more vulnerable to dislodgement than large clumps. Dislodgement often implies removal from the mussel beds into suboptimal habitats with high risk of predation and low food availability. Hence, mussel mortality is linked to the persistence of clumps formed by the self-organization process, and clump persistence thereby influences the selection of particular traits. Hence, a loop develops, where the ecological process of pattern formation adjusts selection processes acting upon the mussels, which than in turn alter the ecological process of pattern formation. Adding this group-level mechanism of selection to our model in **Chapter 6** leads to a substantially higher occurrence of the emergence of labyrinth-like patterns than simulations with individual-level selection only. As these patterns are frequently observed in natural mussel beds, these results suggest that multi-level selection is of key importance in the eco-evolutionary feedback that leads to the formation of spatially patterned mussel beds.

My findings demonstrate that eco-evolutionary feedbacks are of great importance for the evolution of traits that trigger spatial self-organization in ecological systems. At the individual level, self-organizing traits such as movement or attachment can evolve through the interplay between evolution of individual behaviour and the spatial complexity of the community. As large-scale, self-organized patterns are generated by the actions of and interactions between individuals, pattern formation is similarly affected by this eco-evolutionary feedback that often involves traits that modify the environment. In more general terms, an organism's behaviour can affect its environment, which in turn influences the fitness of this individual and of others. The eco-evolutionary feedback that arises from the interplay between individual behaviour and spatial patterning can fundamentally alter the mechanisms that drive evolutionary change by generating a group effect on survival, leading to an additional selection process affecting individual fitness. To truly understand ecological and evolutionary processes in nature, it is of key importance to study eco-evolutionary interactions as they develop in the complex settings of the natural world.

Samenvatting

Ruimtelijke patronen in natuurlijke systemen lijken soms ongelooflijk complex. Toch kunnen ze vaak verklaard worden met een paar eenvoudige regels. Grootschalige, complexe ruimtelijke patronen in zelfgeorganiseerde ecosystemen zijn bijvoorbeeld het gevolg van de lokale interacties tussen organismen. Met andere woorden, de complexiteit van het ecosysteem wordt veroorzaakt door de eigenschappen en het gedrag van organismen. Aggregeren in grootschalige patronen kan echter ook de overleving en fitness van de individuen beïnvloeden. Hierdoor kan het patroonproducerende gedrag weer zijn geëvolueerd als een aanpassing aan de door de organismen zelf gegenereerde omgeving door middel van een zogenaamd eco-evolutionair terugkoppelingsproces. Opvallend is dat zowel empirische als theoretische studies over eco-evolutionaire terugkoppelingen in zelfgeorganiseerde ecosystemen ontbreken. In dit proefschrift heb ik onderzoek gedaan naar de interactie tussen ecologische patroonvorming en de evolutie van patroongerelateerde kenmerken zoals beweging en aanhechting.

Ik onderzocht de interactie tussen de evolutie van zelforganiserend gedrag en de resulterende grootschalige patronen door middel van zowel experimenten als computersimulaties. Hiervoor gebruikte ik mosselbanken als belangrijkste modelsysteem. Jonge mossels in mosselbedden op intertidale zandbanken aggregeren in labyrintachtige patronen. Mosselen hebben voldoende buren in hun nabijheid nodig om het risico op predatie en losslaan door golven te verminderen. Om dit te bereiken hechten mosselen zich met hun zogenaamde byssusdraden aan andere individuen en vormen daarbij dichte kluwens. Om de competitie voor voedsel – algen – te verminderen, moet er echter genoeg open ruimte tussen de kluwens aanwezig zijn. Doordat voedselconcurrentie een effect heeft over een grotere afstand dan het lokale hechten aan buren, ontstaan zelfgeorganiseerde patronen in het mosselbed in de vorm van regelmatige labyrintachtige structuren. De vorming van de patronen verhoogt de dichtheid van mosselen binnenin de mosselklomp terwijl de dichtheid op grotere schaal laag genoeg blijft om voedselconcurrentie te voorkomen. Twee gedragskenmerken zijn de belangrijkste factoren in de vorming van de patronen: beweging en aanhechting. Zonder beweging kunnen mosselen niet aggregeren en zonder hechting van byssusdraden aan nabij liggende buren zal de gegenereerde ruimtelijke structuur niet lang bestaan, aangezien losse individuen gemakkelijk door de golven kunnen worden weggespoeld. Het onderzoeken van de terugkoppeling tussen mosselbedvorming en de evolutie van beweging en aanhechting kan ons interessante inzichten opleveren in de implicaties van eco-evolutionaire interacties in zelf-georganiseerde ecosystemen.

Gedurende de experimenten werd duidelijk dat mosselen gebruikmaken van een speciale bewegingsstrategie. De bewegingspatronen van solitaire mosselen zijn vergelijkbaar met een Lévy walk, waarin veel korte “stapjes” afgewisseld worden met lange, nagenoeg rechtlijnige, bewegingen. Lévy bewegingen worden frequent waargenomen in de natuur, bijvoorbeeld in mariene roofdieren en mieren. Theoretische modellen suggereren echter dat de omstandigheden waarin deze Lévy bewegingen optimaal zijn juist zeer zeldzaam zijn. In **Hoofdstuk 2** beargumenteer ik dat het voorkomen van Lévy-achtige bewegingen in mosselbedden het gevolg is van eco-evolutionaire terugkoppeling tussen patroonvorming en de ontwikkeling van de bewegingsstrategie van de mossel. Om deze hypothese te onderbouwen simuleerde ik de vorming van mosselbedden met een model dat gebaseerd is op individueel gedrag (een ‘individual-based model’), waarin ik de bewegingsstrategie van de virtuele mossels varieerde tussen de verschillende simulaties. Uit de resultaten van deze simulaties blijkt dat patronen het snelst gevormd worden wanneer de mosselen gebruikmaken van een Lévy walk. Een evolutionaire analyse, waarin ik getest heb welke mutant strategieën kunnen binnendringen in een bestaande populatie, wijst uit dat de Lévy walk van nature evolueert in mosselbedden met patronen. De reden hiervoor is dat de Lévy walk de patroonvorming versnelt en het ruimtelijk patroon op zijn beurt de overlevingskansen van de Lévy-mossels verhoogt. Dit resultaat suggereert dat, in mosselbedden, Lévy bewegingen evolueren als gevolg van een sterke interactie tussen ecologische en evolutionaire processen. Hoewel mijn model specifiek van toepassing is op mossels in zelfgeorganiseerde mosselbanken, kunnen de conclusies uit deze studie wellicht ook toepasbaar zijn voor andere organismen en ecosystemen.

Ondanks het toenemende aantal observaties van Lévy bewegingen in de natuur vinden empirici ook regelmatig dat organismen een Lévy walk in de ene omgeving doen maar een Brownse beweging in een andere. Lévy bewegingspatronen worden vaak waargenomen bij organismen die op zoek zijn naar voedsel in arme habitats, terwijl Brownse bewegingspatronen, die bestaan uit stappen van steeds ongeveer dezelfde grootte, voornamelijk in voedselrijke gebieden voorkomen. Dit fenomeen wordt vaak uitgelegd als een actieve verandering in bewegingsstrategie waarmee de zoekefficiëntie in beide omgevingen geoptimaliseerd wordt. In **Hoofdstuk 3** laat ik zien dat, in tegenstelling tot de bovengenoemde visie, de intrinsieke bewegingsstrategie van mossels niet verandert bij verschillende omgevingsomstandigheden, maar dat het waargenomen bewegingspatroon het gevolg is van interacties met omgevingsobjecten zoals andere mosselen. Hierbij moet opgemerkt worden dat mossels niet zoeken naar voedsel, maar naar soortgenoten om zich aan vast te hechten. Door middel van analyses van de bewegingen van mossels in experimenten met verschillende mosseldichtheden, vond ik dat botsingen met andere mosselen de beweging van mossels beïnvloeden, waarbij voornamelijk lange bewegingen afgebroken worden. Door middel van het analyseren van mosselbewegingen in vijf verschillende dichtheden, laat ik zien dat de waargenomen bewegingspatronen daardoor meer op de Brownse patronen gaan lijken met toenemende mosseldichtheid. Ik heb geverifieerd dat deze verschuiving naar Brownse bewegingspatronen wordt veroorzaakt door botsingen met soortgenoten met een simpele analyse, waarbij ik de onafgebroken en afgebroken stappen uiteenhaal. Hieruit blijkt dat het bewegingspatroon niet verandert wanneer alleen de onafgebroken stappen bekeken worden. Met simulaties liet ik zien dat een actieve verschuiving van Lévy naar Brownse beweging met toenemende dichtheid onnodig is, aangezien de Lévy strategie even efficiënt is als de Brownse bewegingsstrategie bij hoge dichtheden. Verder heb ik mijn hypothese, dat elke strategie meer Brown-achtig wordt met toenemende botsingen, analytisch onderbouwd met behulp van een eenvoudig wiskundig argument. Deze conclusies kunnen grote gevolgen hebben voor de manier waarop de beweging van dieren geïncorporeerd wordt in ecologische modellen: het gebruik van een simpele Brownse beweging als een standaard template voor de beweging van dieren is niet altijd gerechtvaardigd en zou vervangen moeten worden door een realistisch, dichtheid-afhankelijk bewegingstype.

Er is momenteel veel discussie gaande over de vraag of Lévy walks die waargenomen zijn in de natuur, daadwerkelijk Lévy walks zijn of dat ze ontstaan zijn uit een mix van meerdere bewegingsstrategieën. Traditionele methoden die gebruikt worden om Lévy walks te ontdekken kunnen geen onderscheid maken tussen echte Lévy walks en de zogenaamde 'composite Brownian walks', In **Hoofdstuk 4** wordt een nieuwe methode gedemonstreerd die helpt om vast te stellen om welke van de twee bewegingsstrategieën het gaat. Deze methode houdt in dat de positie van clusters van kleine bewegingen vergeleken wordt met de aanwezigheid van voedsel op deze plekken (wat indicatief is voor een composite Brownian walk). Met een experiment met slakjes die op algen grazen hebben we aangetoond dat kleine-bewegings-clusters niet alleen voorkomen in voedselrijke gebieden maar ook op de kale grond, wat demonstreert dat Lévy walks daadwerkelijk kunnen bestaan in de natuur.

Mosselen, net als vele andere organismen, aggregeren actief in groepen, alwaar zij samenwerken met soortgenoten. Omdat deze samenwerking, ook wel coöperatie genoemd, misbruikt kan worden door individuen die geen bijdrage leveren, blijft het wijdverspreide gebruik van coöperatie in de natuur een puzzel. Theoretische studies hebben aangetoond dat de ruimtelijke structuur van een populatie de evolutie van coöperatie kan promoten. Maar deze studies beschouwen lokale verspreiding als een belangrijke voorwaarde voor de evolutie van coöperatie, daarbij uit het oog verliezend dat vele soorten zich verspreiden over grote afstanden en toch lokaal coöpereren. In **Hoofdstuk 5** toon ik aan hoe ruimtelijke structuren invloed hebben op de evolutie van investering in byssusdraden in ruimtelijk gestructureerde mosselbedden. Met behulp van een simpel model toon ik aan dat patroonvorming in mosselpopulaties het toch mogelijk maakt dat coöperatief gedrag evolueert en resulteert in een hoge mate van coöperatie in een breed scala van omgevingsstress. Deze resultaten suggereren dat actieve clustering de evolutie van samenwerking kan bevorderen, zelfs wanneer nageslacht wijd verspreid wordt.

Samenwerking en aggregatieve beweging zijn twee fundamentele gedragingen die de basis van zelforganisatie in mosselbanken vormen. Zonder actieve bewegingen die leiden tot het vormen van clusters zijn mosselen niet in staat hun byssusdraden te hechten aan naburige soortgenoten, en zonder samenwerking zou het aggregeren in clusters een nutteloze inspanning zijn. Omdat beweging en coöperatief gedrag zeer afhankelijk zijn van elkaar, zal de evolutie van een van deze eigenschappen waarschijnlijk door het beïnvloeden van het ruimtelijk patroon ook de evolutie van de andere eigenschap beïnvloeden. In **Hoofdstuk 6** van dit proefschrift heb ik laten zien dat de gezamenlijke evolutie van het aanhechtings- en bewegingsgedrag kan resulteren in een ander patroon op mosselbank-niveau dan wanneer slechts een van de eigenschappen op zichzelf staand evolueert. In de meeste evolutionaire modellen wordt co-evolutie van meerdere eigenschappen binnen hetzelfde organismen gewoonlijk buiten beschouwing gelaten; mijn resultaten tonen aan dat dit kan leiden tot het trekken van de verkeerde conclusies.

Het zelfgeorganiseerde patroon dat naar voren komt uit de beweging en de aanhechting van de individuen heeft een belangrijk effect op de overlevingskansen van mossels binnen de mosselklompen. Met een eenvoudig veldexperiment liet ik zien dat niet alleen individuele mosselen losgeslagen kunnen worden door golfslag of predatie, maar dat de overleving voor een belangrijk deel wordt bepaald door het al of niet losslaan van de klomp waarin individuele mossels zich bevinden. Mijn experimenten lieten daarbij zien dat kleine mosselklompen meer kwetsbaar zijn voor het losraken dan grote klompen. Het losraken impliceert vaak verwijdering uit mosselbanken en verhoogt de kans dat de mosselen in een suboptimale omgeving met een hoog risico op predatie en lage beschikbaarheid van voedsel terecht komen. Hierdoor is mosselsterfte verbonden met de standvastigheid van klompen die gevormd zijn door zelforganisatie; deze klompen beïnvloeden daardoor selectie van specifieke eigenschappen. Hierbij ontstaat een terugkoppeling waarin het ecologische proces van patroonvorming de evolutionaire selectieprocessen beïnvloedt, die dan op hun beurt het ecologische proces van patroonvorming aanpassen. Het toevoegen van dit selectiemechanisme op groepsniveau aan ons model in **Hoofdstuk 6** geeft een heel interessant resultaat. Zonder dit selectiemechanisme op groepsniveau kunnen slechts voor een heel beperkt aantal parameterwaardes de vorming van de labyrintachtige patronen verklaard worden. Meestal vormen er zich dan losse klompjes, of blijven de mossels willekeurig verspreid. Met selectie op groepsniveau vormen zich voor nagenoeg alle parameterwaardes de geobserveerde labyrintachtige patronen. Deze labyrintachtige patronen worden vaak waargenomen in natuurlijke mosselbanken, wat suggereert dat multi-level selectie van groot belang is in de eco-evolutionaire interactie die leidt tot de vorming van ruimtelijke patronen in mosselbanken.

Mijn bevindingen tonen aan dat eco-evolutionaire terugkoppelingen van groot belang zijn voor het ontstaan van ruimtelijke patronen in zelfgeorganiseerde ecosystemen. Op individueel niveau kunnen zelforganiserende eigenschappen, zoals beweging of aanhechting, evolueren door de wisselwerking tussen de evolutie van het individuele gedrag en de ruimtelijke complexiteit van de gemeenschap. Deze grootschalige, zelfgeorganiseerde patronen worden op hun beurt gegenereerd door de acties van en interacties tussen individuen; er is daarom duidelijk sprake van een eco-evolutionaire feedback. Deze interactie vindt hoogstwaarschijnlijk niet alleen plaats in ecosystemen met zelforganiserende, regelmatige patronen, zoals mosselbedden, maar zal waarschijnlijk plaatsvinden in elk ecosysteem waar organismen zelf hun ruimtelijke verdeling beïnvloeden. In meer algemene termen kunnen we zeggen dat wanneer het gedrag van een organisme invloed heeft op zijn omgeving, deze omgeving op zijn beurt de fitness van zowel dit individu als dat van anderen zal beïnvloeden. De eco-evolutionaire terugkoppeling die voortvloeit uit het samenspel tussen individueel gedrag en ruimtelijke patroonsvorming kan de evolutionaire mechanismen fundamenteel veranderen, bijvoorbeeld door verschillen tussen groepen te genereren welke kunnen leiden tot selectie op een hoger niveau dan het individu. Om de eigenschappen van organismen in de complexe natuur goed te doorgronden is het van cruciaal belang inzicht te krijgen in de interactie tussen ecologische en evolutionaire processen, ook in systemen waar de relatie tussen organismen en de ruimtelijke structuur van het ecosysteem minder rechtlijnig is.

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To be honest, I have been procrastinating immensely when writing my acknowledgements. I think this has something to do with the facts that (i) the acknowledgements will probably be the most frequently read part of my thesis, while (ii) it is also the part that is most error-prone. Though I do not take your help and kindness for granted, my memory is flawed sometimes (here I can already say thanks, because I'm quite sure I owe this to my children), and making a list of all people who I would like to acknowledge for their help of any sorts over the last years is quite a challenge. Here, at last, is my attempt to thank you all; please do not be disappointed if your name is nowhere to be found.

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About the author

My name is Monique de Jager-Out and I′m the author of this dissertation. I was born in the early hours of a beautiful winter's day in 1984 in a small suburban town south of Rotterdam, the Netherlands, as the beloved second daughter of Henk de Jager and Gré de Jager-Jonas. Pretty much my entire youth I spend in this town, Spijkenisse; my preschool, primary school, and high school were all within biking distance of my home. Even my husband Mark was born here; we met at a high school graduation party and never really parted again. Like many small suburban towns, Spijkenisse is devoid of universities; therefore, I commuted to Leiden instead, where I studied biology from 2003 to 2008. For my bachelor thesis I investigated the spatial dynamics of a prisoner's dilemma (a cooperation game where cheating can be advantageous), my first master project involved developing a website for photo-identification of humpback whales, and for my second master project I spend three months in Cameroon to investigate the spatial distribution of large carnivores. During my time in Leiden, I developed an interest in eco-evolutionary dynamics, spatial processes, and individual-based modelling. One of the researchers there gave me the advice to stop investigating cute and fluffy big animals (meaning whales and lions) and start focusing on the less attractive organisms, if I ever would like to be taken seriously. Hence, when the vacancy of PhD-student at the NIOO-CEME popped up, I immediately replied. From 2008 to 2012, I worked full-time at the NIOO-CEME (now NIOZ Yerseke). After my son Logan was born in July 2012, I was on maternity leave until October and started working again part-time on a scholarship of the RUG. Although my thesis wasn't finished, we moved to Zürich, Switzerland, in 2013, where I worked as a postdoctoral researcher at the plant ecology group of the ETH. Raising two kids in a foreign country is exponentially more difficult than raising one, so soon after the birth of our daughter Caitlin in August 2014, we moved back to the Netherlands, where I am now working as a postdoctoral researcher at the ecology and biodiversity group of Utrecht University.

List of publications

A. Kölzsch, A. Alzate, F. Bartumeus, **M. de Jager**, E.J. Weerman, G.M. Hengeveld, M. Naguib, B.A. Nolet, J. van de Koppel (2015). Experimental evidence for inherent Lévy search behaviour in foraging animals. *Proceedings of the Royal Society B* **282**, 20150424.

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